

Changing Ecosystem Dynamics in the Laurentian Great Lakes: Bottom-Up and Top-Down Regulation

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Understanding the relative importance of top-down and bottom-up regulation of ecosystem structure is a fundamental ecological question, with implications for fisheries and water-quality management. For the Laurentian Great Lakes, where, since the early 1970s, nutrient inputs have been reduced, whereas top-predator biomass has increased, we describe trends across multiple trophic levels and explore their underlying drivers. Our analyses revealed increasing water clarity and declines in phytoplankton, native invertebrates, and prey fish since 1998 in at least three of the five lakes. Evidence for bottom-up regulation was strongest in Lake Huron, although each lake provided support in at least one pair of trophic levels. Evidence for top-down regulation was rare. Although nonindigenous dreissenid mussels probably have large impacts on nutrient cycling and phytoplankton, their effects on higher trophic levels remain uncertain. We highlight gaps for which monitoring and knowledge should improve the understanding of food-web dynamics and facilitate the implementation of ecosystem-based management.

Keywords: *invasive species, wasp-waist ecosystems, multiple stressors, regime shift, trophic cascade*

The importance of top-down (i.e., driven by predation) and bottom-up (i.e., driven by limited resources) forcing to ecosystem structure has been a fundamental question in ecology since the influential works of Forbes (1887) and Hairston and colleagues (1960), among others. These forces can be important, even interdependent, within ecosystems (e.g., Carpenter et al. 1985, Menge 2000, Gruner et al. 2008), and stressors, such as eutrophication or overfishing, can shift the dominant drivers of an ecosystem (e.g., Lotze and Milewski 2004, Daskalov et al. 2007). Furthermore, ecosystems that exhibit top-down control may undergo trophic cascades within the constraints of system productivity (Carpenter et al. 1985); a typical example of such a cascade is when tertiary consumers increase, which causes secondary consumers to decline, thus allowing primary consumers to increase and, ultimately, primary producers to decline. Although such cascading effects can be intentionally used as a management tool (e.g., Shapiro and Wright 1984, DeMelo et al. 1992), they can also occur unintentionally, such as when overfishing caused a regime shift in the Black and Baltic Seas that had negative ecological and economic consequences (Daskalov et al. 2007, Casini et al. 2009). Therefore, for exploited aquatic ecosystems, resource managers and

ecologists have a mutual interest in understanding the relative importance of top-down and bottom-up forcing.

Assessing the importance of these key drivers can be difficult in large ecosystems, in which logistical considerations preclude the experimental approaches that have been used in smaller ecosystems. Instead, the analysis of long-term (i.e., time-series) data offers a solution; positive correlations between adjacent trophic levels indicate bottom-up control (i.e., more resources support more consumers), whereas negative correlations between adjacent trophic levels indicate top-down control (i.e., more predators reduce prey resources). Such analyses provided important ecological understanding in estuarine and marine systems, such as the eastern Scotian Shelf of the North Atlantic (Frank et al. 2005), the Baltic Sea (Casini et al. 2009), and the Black Sea (Daskalov et al. 2007), but have not yet been applied to the world's freshwater "inland seas," such as the Great Lakes of North America and the Great Lakes of eastern Africa.

The Laurentian Great Lakes of North America are particularly amenable to this correlative approach, for several reasons. First, the lakes (Superior, Michigan, Huron, Erie, and Ontario) have been monitored for nutrients, plankton, fish, and other physicochemical attributes since as far back as the

mid-1970s for some trophic levels; since 1998, nearly complete data sets of this type have been available for all of them (with the exception of nonindigenous dreissenid mussels). Second, because the characteristics of these lakes (e.g., productivity, thermal structure, size, depth, prevalence of nonindigenous species) span wide gradients, interlake comparisons can be used to test predictions developed in other large ecosystems. For example, in a meta-analysis from the North Atlantic, Frank and colleagues (2007) found that cooler waters with fewer species were more associated with top-down control, whereas warmer, species-rich waters tended to be associated with bottom-up forcing. Third, for a subset of the Great Lakes, a growing discussion among scientists and managers has emerged regarding the importance of bottom-up and top-down drivers. An accumulation of biomass of top predators (i.e., piscivorous fish) in several of the lakes has raised concerns that consumption by top predators is unsustainable for preferred prey fish species (Stewart DJ et al. 1981, Jones et al. 1993, Rand and Stewart 1998, Bence et al. 2008, Murry et al. 2010). In addition, the total phosphorus (TP) in offshore waters has been declining in several lakes; therefore, oligotrophication may underlie declines in phytoplankton, zooplankton, and even changes to fish community composition (Ludsin et al. 2001, Vanderploeg et al. 2010, Barbiero et al. 2011). Finally, since 2010, these lakes have been the beneficiaries of more than \$1 billion in US funding that was intended to accelerate restoration by improving habitat (e.g., removing contaminants, further reducing TP inputs, restoring wetlands) and combating or preventing the invasion of nonindigenous species, among other goals (WHCEQ 2010).

In the present study, we compiled time-series data across multiple trophic levels and physicochemical attributes for each of the Laurentian Great Lakes. Given the breadth of this overview and our interest in detecting ecosystem-level trends, we pooled the data at the community level for each trophic level when that was possible. Our first goal was to determine whether trends could be detected within a given lake. Second, we assessed whether bottom-up or top-down regulation was occurring in each lake by estimating the correlation coefficient between the time-series data of adjacent trophic levels. Third, we identified common results across the Great Lakes and explored similarities with other large ecosystems. Finally, we identified important information or monitoring gaps and avenues for future research that would improve the management and restoration of these water bodies, which provide numerous ecosystem services to the 30 million people that live within their watersheds.

Great Lakes food webs: A legacy of perturbations and restoration successes

Although the Laurentian Great Lakes (figure 1) share a similar geologic history, table 1 describes how they vary in size, productivity, and exposure to human-induced perturbation (particularly nonindigenous species). For example, Lake Superior represents extremes in all three of the above

categories. It is the largest, deepest, and coldest of the lakes and is the least perturbed, in part because of the inability of several nonindigenous species (e.g., dreissenid mussels, alewife [*Alosa pseudoharengus*]) to proliferate because of its inhospitable abiotic conditions and the relatively quick response by managers to control sea lamprey (*Petromyzon marinus*; Christie and Goddard 2003). Lake Superior also has the lowest species richness for fishes among the Great Lakes (approximately 52 species; Hubbs and Lagler 2004). At the other extreme, Lake Erie is the shallowest, warmest, and most biologically productive (containing about 85 fish species; Hubbs and Lagler 2004). Given the predictions put forth by Frank and colleagues (2007), one would expect that Lake Superior would exhibit the most evidence of top-down regulation, whereas Lake Erie (especially the western basin) would exhibit the most evidence of bottom-up regulation. The other three lakes (Huron, Michigan, and Ontario) support numerous nonindigenous species (table 1b), and their depth, thermal structure, and fish species richness (approximately 69, 68, and 64 species, respectively; Hubbs and Lagler 2004) fall between those for Superior and Erie. In terms of their trophic state (using April TP concentrations as a proxy), the offshore waters of Lake Huron have been even more oligotrophic than those of Lake Superior since 2008, whereas those of Lakes Michigan and Ontario have been 35% and 117% higher, respectively. The expectations for these intermediate lakes are less clear; however, one might expect a mix of top-down and bottom-up regulation within the food web.

Anthropogenic perturbations to the Great Lakes ecosystems began as far back as the early 1800s, when dams were first constructed along their tributaries (Trautman 1982). During the 1900s, nearshore and tributary habitats suffered further damage as demand for lumber and agriculture from a growing human population led to the deforestation of watersheds and dewatering of wetlands (Beeton et al. 1999). Commercial fishing for lake trout (*Salvelinus namaycush*) and their prey fishes (ciscoes) was well developed by the 1880s (Eshenroder and Lantry 2013), and technological advances permitted increased exploitation through the early twentieth century, when the effects of overfishing became apparent. In fact, three native deepwater prey fishes (*Coregonus nigripinnis*, *Coregonus johanna*, *Coregonus reighardi*) are now extinct in the five Great Lakes, primarily because of overfishing. The proliferation of nonindigenous species began in the late 1800s, as alewife and sea lamprey became abundant in Lake Ontario (although whether these species from the Atlantic Ocean were also native to Lake Ontario is debated; see Eshenroder and Lantry 2013). Improvements to the Welland Canal in the early twentieth century allowed sea lamprey and alewife to bypass Niagara Falls and move into Lake Erie, which then allowed them access to the entire basin. The devastation wrought by parasitic sea lamprey on native top predators catalyzed the United States and Canada to ratify the Convention on Great Lakes Fisheries in 1955, which initiated a binational sea lamprey control program (Christie and Goddard 2003). The synergistic effects of alewife and sea



Figure 1. Satellite image of the Laurentian Great Lakes. The yellow line denotes the US–Canada border, and the names of states and provinces within the watershed are identified. Source: Figure created by David Bennion from Bing Maps; Microsoft product screen shots reprinted with permission from Microsoft Corporation.

Table 1a. Physicochemical attributes of important nonindigenous species in the Laurentian Great Lakes, including the three basins of Lake Erie, between 1998 and 2010.

Attribute	Superior	Huron	Michigan	Western Erie	Central Erie	Eastern Erie	Ontario
Surface area (in square kilometers)	82,100	59,600	57,800	3340	16,185	6166	18,960
Mean depth (in meters)	147	59	85	7	19	24	86
April total phosphorus (in micrograms per liter)	2.1	2.5	3.8	32.2	13.9	9.7	5.3

Table 1b. The relative abundance of important nonindigenous species in the Laurentian Great Lakes, including the three basins of Lake Erie, between 1998 and 2010.

Species	Superior	Huron	Michigan	Western Erie	Central Erie	Eastern Erie	Ontario
<i>Dreissena</i> spp.	Rare	Abundant	Abundant	Abundant	Abundant	Abundant	Abundant
<i>Bythotrephes longimanus</i>	Limited or variable	Abundant	Abundant	Limited or variable	Abundant	Abundant	Limited or variable ^a
<i>Cercopagis pengoi</i>	Rare	Rare	Limited or variable	Rare	Limited or variable	Limited or variable	Abundant
Round goby	Rare	Abundant	Abundant	Abundant	Abundant	Abundant	Abundant
Alewife	Rare	Rare ^b	Abundant	Limited or variable	Limited or variable	Abundant	Abundant

^aIncreasingly abundant since 2005. ^bSince 2004.

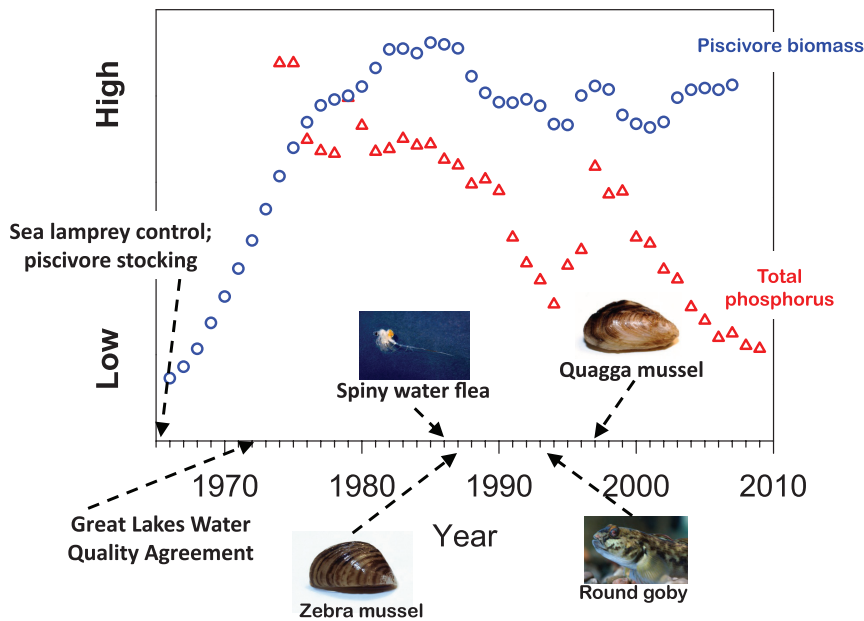


Figure 2. Generalized time line of major events in Lake Michigan since 1965. The photographs are of species that have successfully invaded (an arrow approximates their first discovery) and proliferated in the middle of the food web in the 1980s and 1990s and that have been hypothesized to alter energy transfer pathways: spiny water flea (*Bythotrephes longimanus*), zebra mussel (*Dreissena polymorpha*), quagga mussel (*Dreissena bugensis*), and round goby (*Neogobius melanostomus*). The data points (a 3-year running average is plotted, but the axis values are not shown, for simplicity) display offshore total phosphorus concentrations (the red triangles; data from Madenjian et al. 2002), which have declined since 1972, when the Great Lakes Water Quality Agreement was signed. Also depicted is total piscivore biomass (the blue circles), which increased between 1965 and 1986 because of the control of nonindigenous sea lampreys (*Petromyzon marinus*) and successful state and federal stocking initiatives and which, since 1987, has remained relatively stable. Photographs: Michigan Sea Grant.

lamprey reverberated throughout the Great Lakes ecosystem. For example, after sea lamprey and overfishing decimated top predators in Lake Michigan, alewives proliferated in the 1960s and selectively preyed on larger zooplankton. In turn, the zooplankton community shifted from large-bodied to small-bodied copepods and herbivorous cladocerans (Wells 1970), and grazing rates on phytoplankton declined (Kitchell and Carpenter 1987). A final important perturbation was an increase in inputs of contaminants and nutrients (especially TP) following World War II, which led to shifts in zooplankton and benthos communities (Beeton 1965), the development of nuisance cyanobacteria populations (Davis 1964), reductions in dissolved oxygen concentrations (Beeton 1965), and a loss of habitat for cool- and coldwater fishes (Beeton et al. 1999). The effects of eutrophication, which were most pronounced in Lake Erie, led to the 1972 signing of the binational Great Lakes Water Quality Agreement.

Through management actions, these ecosystems were partly restored by the 1980s. Sea lamprey control resulted in populations that were only a fraction of their peak densities

(Christie and Goddard 2003), and this enabled the successful introduction of other salmonines (e.g., Chinook salmon [*Oncorhynchus tshawytscha*], brown trout [*Salmo trutta*], coho salmon [*Oncorhynchus kisutch*], rainbow trout [*Oncorhynchus mykiss*]) and the reintroduction of lake trout in the 1960s and 1970s. These stocking programs created popular recreational fisheries and led to the buildup of piscivore biomass that controlled nuisance alewife populations (e.g., Madenjian et al. 2008), which, in turn, enabled the zooplankton community to return to a structure similar to that before the 1960s (Scavia et al. 1986). Eutrophication effects were also reversed as a result of the Great Lakes Water Quality Agreement, which reduced point-source inputs of TP (Beeton et al. 1999) and helped set the stage for bottom-up regulation to possibly play a more important role in subsequent decades.

Just as these positive changes were becoming apparent in the lakes during the 1980s and 1990s, a new wave of non-indigenous species arrived in ballast water from transoceanic ships. These invaders spanned multiple trophic levels and included benthic, filter-feeding zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*, respectively); planktonic predatory zooplankton species (i.e., *Cercopagis pengoi*, *Bythotrephes longimanus*); and a benthivorous prey fish (i.e., round goby [*Neogobius melanostomus*]). Each of these species has influenced food-web dynamics and complicated the interpretations of top-down and bottom-up drivers during its proliferation through the 1990s and 2000s. In particular, dreissenid mussels affected both abiotic (e.g., enhanced water clarity and altered nutrient cycling) and biotic (e.g., reduced phytoplankton and microzooplankton, enhanced benthic algae and macrophytes, altered benthic macroinvertebrate community composition) components of the ecosystem (for reviews, see Vanderploeg et al. 2002, Hecky et al. 2004), including a facilitation of the expansion of round gobies (Vanderploeg et al. 2002).

As a result, by the late 1990s, management agencies became increasingly concerned about the balance of predator and prey in Great Lakes ecosystems, given the “new” invaders in the middle of the food web, oligotrophication at the base of the food web, and the buildup of piscivorous fish at the top. Figure 2 demonstrates the time line of these events in Lake Michigan. Furthermore, by the 2000s, up to 80% of some nonindigenous salmonine species (e.g., Lake Huron

Table 2. Spearman's rank correlations between specific biotic or physicochemical attributes and the year in each of the five Laurentian Great Lakes, including the three basins of Lake Erie.

Attribute	Superior	Huron	Michigan	Western Erie	Central Erie	Eastern Erie	Ontario
Total phosphorus (TP) inputs	.23	-.35	-.20	.34	.46	.70*	.35
April TP concentrations	.35	-.72 ^b *	-.95*	.19	.12	.23	.19
April water clarity	.69*	.93*	.81*	.30	-.09	-.10 ^b	.69*
May chlorophyll a	-.77*	-.93*	-.94*	-.01	.51	.02	.07
March–November chlorophyll a	-.42	-.95*	-.82*	.19	.75*	.45	.26
Zooplankton	-.24 ^b	-.87*	-.67	.44	.59	-.29	-.88 ^b *
Benthic macroinvertebrates ^a	.27	-.69*	-.79*	.87*	.75*	.37	-.95*
Prey fish	-.80*	-.75*	-.91 ^b *	.20	-.20	–	-.31
Piscivore	-.09	-.34 ^b	.63*	–	.64* ^c	–	–1.00*
Piscivore stocking	-.65*	-.88*	.04	–	–	–	.15
Sea lamprey	-.38	-.41	-.09	–	.50 ^c	–	.46

Note: Each time series spans the years 1998–2010, and the supplemental material shows the missing years within this span. ^aThis table does not include dreissenid mussels. ^bSignificant ($p < .05$) temporal autocorrelation detected. ^cThis value is for all three basins of Lake Erie. * $p < .05$.

Table 3. Spearman's rank correlations between adjacent trophic levels (or key physicochemical attributes) to explore evidence for bottom-up (positive correlation) or top-down (negative correlation) regulation in each of the five Laurentian Great Lakes, including the three basins of Lake Erie.

Correlation	Superior	Huron	Michigan	Western Erie	Central Erie	Eastern Erie	Ontario
May chlorophyll a × April total phosphorus (TP)	-.39	.63*	.88*	.40	.04	.53	.20
March–November chlorophyll a × April TP	-.69*	.74*	.77*	.31	.24	.32	.01
Zooplankton × May chlorophyll a	.09	.92*	.74*	.17	.21	-.26	.35
Zooplankton × March–November chlorophyll a	-.09	.78*	.60	.18	.28	.00	.38
Prey fish × zooplankton	.74*	.93*	.67	-.32	.15	–	.33
Prey fish × nondreissenid benthos	-.35	.57	.74*	.31	-.15	–	.24
Piscivore biomass × prey fish	.25	.71*	-.75*	.57*	.10	–	.67*

Note: Each time series spans the years 1998–2010, and the supplemental material shows the missing years within this span. * $p < .05$.

Chinook salmon; Johnson et al. 2010) were of wild—rather than hatchery—origin as they further exploited Great Lakes tributaries for spawning habitat. Until this percentage was realized, the piscivore biomass in Lakes Huron, Michigan, and Ontario was greatly underestimated.

Data set description and analysis

Data were aggregated lakewide from a variety of published and unpublished data sources (see the supplemental material). Lake Erie was unique in that we analyzed the data within each of its three basins (where that was possible), because of their stark differences in morphometry and productivity (Ludsin et al. 2001). Because of data limitations, we focused on the data from 1998 and thereafter. When longer time series were available, we sought to determine whether patterns held with a larger sample size. Because autocorrelated data sets can increase the type I error rate (i.e., the probability of finding a significant trend or correlation when one does not truly exist), we identified autocorrelated time series by determining whether lagged residuals were correlated (Box and Jenkins 1976); those results are reported

in table 2. We used Spearman's rank correlation analysis ($\alpha = .05$) to determine whether a given trophic level or physicochemical attribute within a lake exhibited a trend over time (also reported in table 2) and to test adjacent trophic levels for top-down (negative correlation) or bottom-up (positive correlation) forcing (reported in table 3). When we examined the correlations between adjacent trophic levels, no adjustment to remove autocorrelation from a time series was required, because only one time series exhibited autocorrelation in any pair (Casini et al. 2009). We did not conduct correlations between adult sea lamprey and piscivores, because either one or both of these trophic levels were manipulated by managers (i.e., killing of sea lampreys or stocking of piscivores) in each lake. Even though piscivore trends were influenced by stocking in all of the lakes but Superior and Erie, we argue that correlations between piscivores and prey fish are still meaningful from the bottom-up perspective, because the survival of stocked fish can be influenced by the density of prey fish (Warner et al. 2008), and from the top-down perspective, because the realized biomass of piscivores can influence prey fish dynamics.

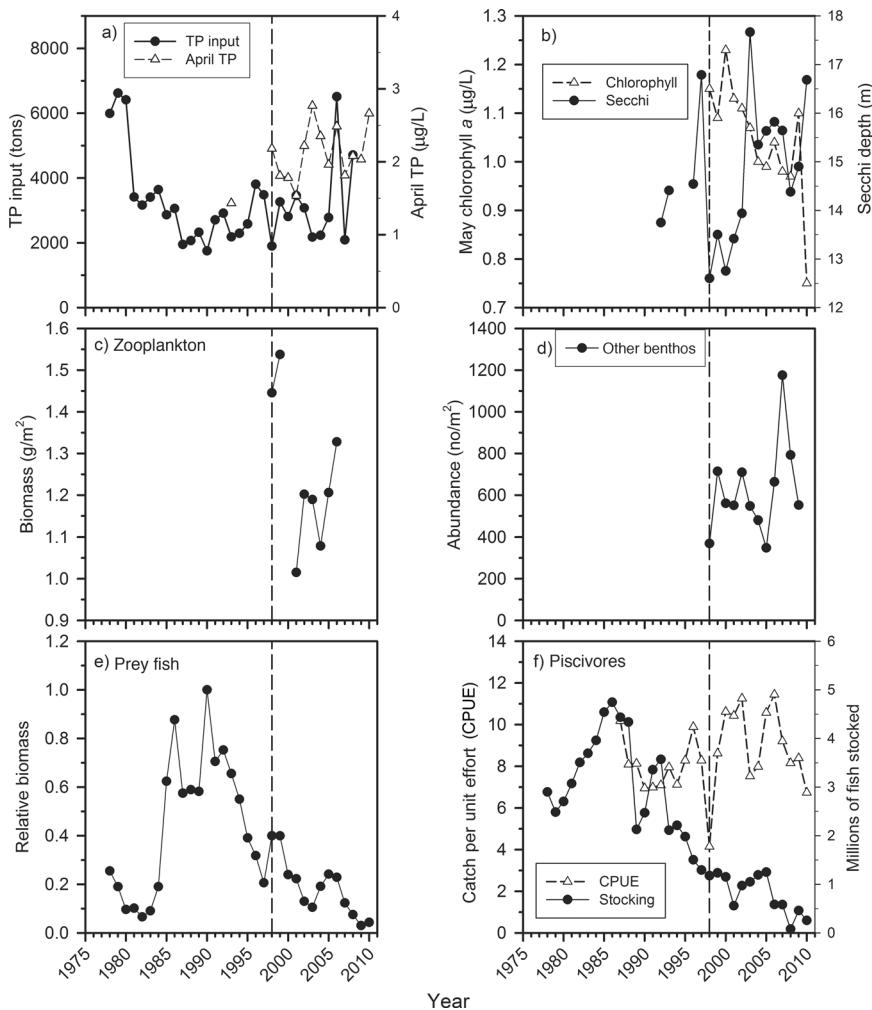


Figure 3. Time series of important physicochemical attributes and trophic levels in Lake Superior. The lengths of the time series vary among the panels. The vertical dashed line at 1998 shows the point after which within-lake Spearman's rank correlations were analyzed. Abbreviations: g/m², grams per square meter; m, meters; no/m², number per square meter; TP, total phosphorus; µg/L, micrograms per liter. For details regarding data sources, see the supplemental material.

Lake-specific trends and trophic relationships

Lake Superior has been relatively stable since 1998; only four time series exhibited linear trends (see table 2, figure 3). At the base of the food web, TP inputs and April TP concentrations were without trend. Even so, reduced concentrations of May chlorophyll *a*, a commonly used proxy for phytoplankton biomass, and enhanced April water clarity (measured by the depth to which a Secchi disk is visible) were evident. The levels of chlorophyll *a* averaged between March and November, however, revealed no negative trend. Crustacean zooplankton biomass and benthic macroinvertebrate densities showed no trends, despite declines in prey fish biomass (which were driven by bloater [*Coregonus hoyi*], cisco, and rainbow smelt [*Osmerus mordax*]). At the top of the food web, the abundance of nonindigenous sea lamprey was without trend, as was that of one of its primary prey,

lean lake trout; unfortunately, no time series exists for the siscowet form of lake trout, which has been estimated to attain a fivefold greater biomass than the lean (Kitchell et al. 2000). The number of stocked lean lake trout has declined since 1998, which followed an earlier trend that began during the late 1980s in response to increased natural reproduction (Hansen 1999).

A comparison between adjacent trophic levels yielded evidence of bottom-up regulation of prey fish through zooplankton. Evidence for top-down control was limited to an inverse correlation between March–November chlorophyll *a* and spring TP (table 3), but we believe that result to be spurious, because phytoplankton production should increase (rather than decline) when its limiting nutrient (TP) becomes more plentiful.

Lake Huron exhibited trends in eight time series since 1998 (see table 2, figure 4). The annual TP input was without trend since 1998 but exhibited a negative trend over the entire time series (1978–2008; $\rho = -0.70$, $p < .0001$, $n = 31$). Concentrations of chlorophyll *a* (both in May and between March and November) have declined since 1998, which is concomitant with increased April water clarity and reductions in April TP concentrations. The biomass of crustacean zooplankton (primarily herbivorous cladocerans and cyclopoid copepods) and nondreissenid benthic invertebrates (primarily the native amphipod *Diporeia* species) also declined. The density of dreissenid mussels was an exception, in that it increased over the 3 years for which data were available. Prey fish biomass declined between 1999 and 2010, with a 98% or greater decline in alewife, deepwater sculpin, and slimy sculpin (*Cottus cognatus*). Finally, neither the biomass of piscivores (pooled lake trout and Chinook salmon) nor the densities of sea lamprey have exhibited trends since 1998. The stocking of piscivores declined, however, between 1998 and 2010, because managers became concerned regarding the imbalance between piscivore consumptive demand and prey fish production and because they gained an improved understanding of the increasing wild reproduction of Chinook salmon (Johnson et al. 2010).

Several adjacent trophic levels in Lake Huron were positively correlated to one another, which is consistent with bottom-up control (table 3). These relationships were

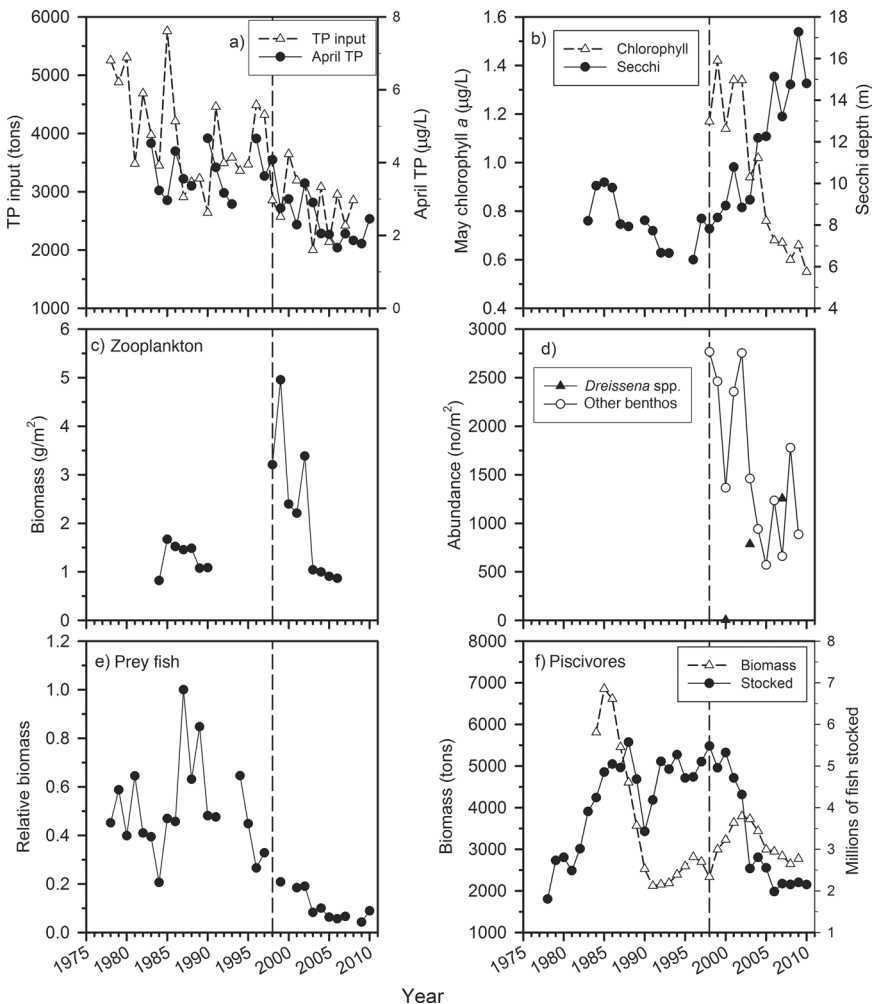


Figure 4. Time series of important physicochemical attributes and trophic levels in Lake Huron. The lengths of the time series vary among the panels. The vertical dashed line at 1998 shows the point after which within-lake Spearman's rank correlations were analyzed. Abbreviations: g/m², grams per square meter; m, meters; no/m², number per square meter; TP, total phosphorus; µg/L, micrograms per liter. For details regarding data sources, see the supplemental material.

evident between piscivores and prey fish, between prey fish and zooplankton, between zooplankton and chlorophyll *a* (averaged in May and averaged between March and November), and between chlorophyll *a* and April TP. When longer time series were analyzed between piscivores and prey fish (1984–2009, $n = 23$) and between prey fish and zooplankton (1984–2006, $n = 15$), no evidence for bottom-up control was observed ($p = .66$ and $p = .28$, respectively). No evidence for top-down control was found in Lake Huron.

Lake Michigan, as did Lake Huron, changed appreciably between 1998 and 2010, with the majority (7 of 11) of the time series' showing a significant trend (see table 2, figure 5). As with Lake Huron, the annual TP inputs exhibited no trend since 1998 (table 2), but a negative trend was documented between 1978 and 2008 ($\rho = -.40$, $p = .03$, $n = 31$). April

TP concentrations and chlorophyll *a* (both in May and between March and November) declined, whereas water clarity increased. Despite reductions in chlorophyll *a*, the crustacean zooplankton biomass exhibited no trend. The density of dreissenid mussels increased dramatically over the 4 years for which estimates were available, whereas those of nondreissenid benthic macroinvertebrates declined (driven by *Diporeia* species). Since 1998, prey fish biomass has trended negatively, with alewife, bloater, rainbow smelt, and deepwater sculpin all declining by at least 70%. In contrast to the rest of the food web, the piscivore biomass (pooled lake trout, Chinook salmon, brown trout, coho salmon, and rainbow trout) increased between 1998 and 2008. The levels of sea lampreys were both variable but without trend.

Unlike in Lake Huron, evidence for both top-down and bottom-up regulation since 1998 was found in Lake Michigan (table 3). As piscivore biomass increased, prey fish biomass declined, which is consistent with top-down control. With the entire time series, however, top-down regulation of prey fish was no longer supported (1978–2008; $\rho = .22$, $p = .24$, $n = 31$). Evidence for bottom-up regulation was present among several trophic pairs. At the base of the food web, chlorophyll *a* (both in May and between March and November) was positively correlated with April TP, whereas higher zooplankton biomass was associated with higher chlorophyll *a* in May but

not between March and November. Finally, prey fish biomass was positively correlated with that of nondreissenid benthic invertebrates.

Lake Ontario exhibited only four linear trends since 1998 (table 2, figure 6). Neither annual TP inputs nor April TP concentrations exhibited any trend. Water clarity increased, although no trend in chlorophyll *a* was detected. The biomass of crustacean zooplankton and of nondreissenid benthic invertebrates declined. Dreissenid mussel density peaked in 2003 but then declined by 2008. Although prey fish biomass exhibited no trend since 1998, a significant decline was evident when the entire time series was considered (1981–2010; $\rho = -.87$, $p < .0001$, $n = 30$). Piscivore biomass declined each year between 1998 and 2007 (lake trout declined by 64% between 1998 and 2007, whereas Chinook salmon declined

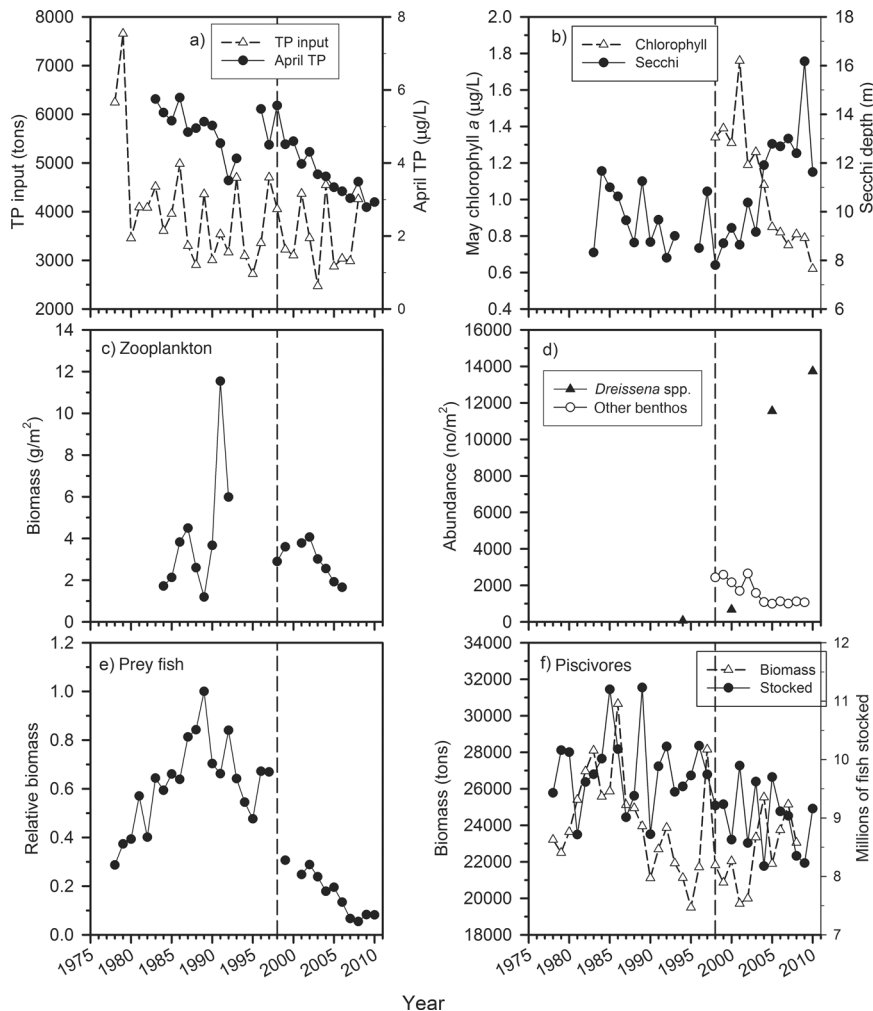


Figure 5. Time series of important physicochemical attributes and trophic levels in Lake Michigan. The lengths of the time series vary among the panels. The vertical dashed line at 1998 shows the point after which within-lake Spearman's rank correlations were analyzed. Abbreviations: g/m², grams per square meter; m, meters; no/m², number per square meter; TP, total phosphorus; µg/L, micrograms per liter. For details regarding data sources, see the supplemental material.

by only 21%). The abundance of sea lamprey and the number of stocked lake trout and Chinook salmon revealed no trend.

The only significant trophic interaction in Lake Ontario indicated that piscivore biomass was limited by prey fish biomass (table 3). We acknowledge the possibility that this bottom-up control was influenced by declines in piscivore stocking. We also note that focusing only on the 1998–2010 period may particularly bias our understanding of ecosystem change in this lake, because strong negative trends in April TP concentrations (1986–1998; $\rho = -.88$, $p = .001$, $n = 10$) and prey fish biomass (1981–1998; $\rho = -.81$, $p < .0001$, $n = 18$) existed before 1998 (prior to the dreissenid mussel proliferation), whereas trends for these variables in the years after 1998 revealed no pattern. On the basis of these results, stronger evidence for bottom-up regulation in Lake Ontario may have existed prior to 1998.

Lake Erie yielded relatively few trends between 1998 and 2010 (table 2, figure 7). For the two trophic levels for which data were available only at the lakewide level, the abundance of piscivores (age 2 and older walleye [*Sander vitreus*]) increased, driven by an unusually strong year class produced in 2003 that fueled relatively large population sizes from 2005 to 2009, whereas the abundance of sea lamprey was without trend. Among the basin-specific data, annual TP inputs exhibited a (positive) trend only in the eastern basin, and no trend in April TP concentrations was detected in any basin. Furthermore, no trend was observed in April water clarity, and a trend in chlorophyll *a* was observed only in the central basin between March and November (a positive one). One caveat is that phytoplankton dynamics, particularly in the western basin, may be responding to inputs of soluble reactive phosphorus, rather than those of TP, and inputs of soluble reactive phosphorus in the western basin have increased since 1995 (OEPA 2010). Nonetheless, the biomass of crustacean zooplankton exhibited no trend since 1998 in any basin, and the densities of nondreissenid benthic invertebrates increased in the western and central basins. The density of dreissenid mussels in the western basin has also increased since 1998 ($\rho = .58$, $p = .048$, $n = 12$); time series for the other basins were not available. Finally, no trend in prey fish biomass was detected for the two basins (i.e., western, central) for which

data were available. The only significant trophic interaction revealed in Lake Erie suggested bottom-up control of piscivorous walleye between 1998 and 2009 (from the western basin prey fish time series, table 3). When this time series was extended to 1978, however, the correlation was no longer significant ($\rho = .07$, $p = .70$, $n = 33$).

Synthesis across lakes, data gaps, and future research possibilities

In this article, we sought to stimulate future research aimed at understanding the mechanisms underlying common trends and trophic interactions in the Laurentian Great Lakes (box 1). Although the ecological snapshot provided here offers arguably the most expansive and synthetic compilation and analysis of physicochemical and ecological data sets from all five Laurentian Great Lakes, we acknowledge

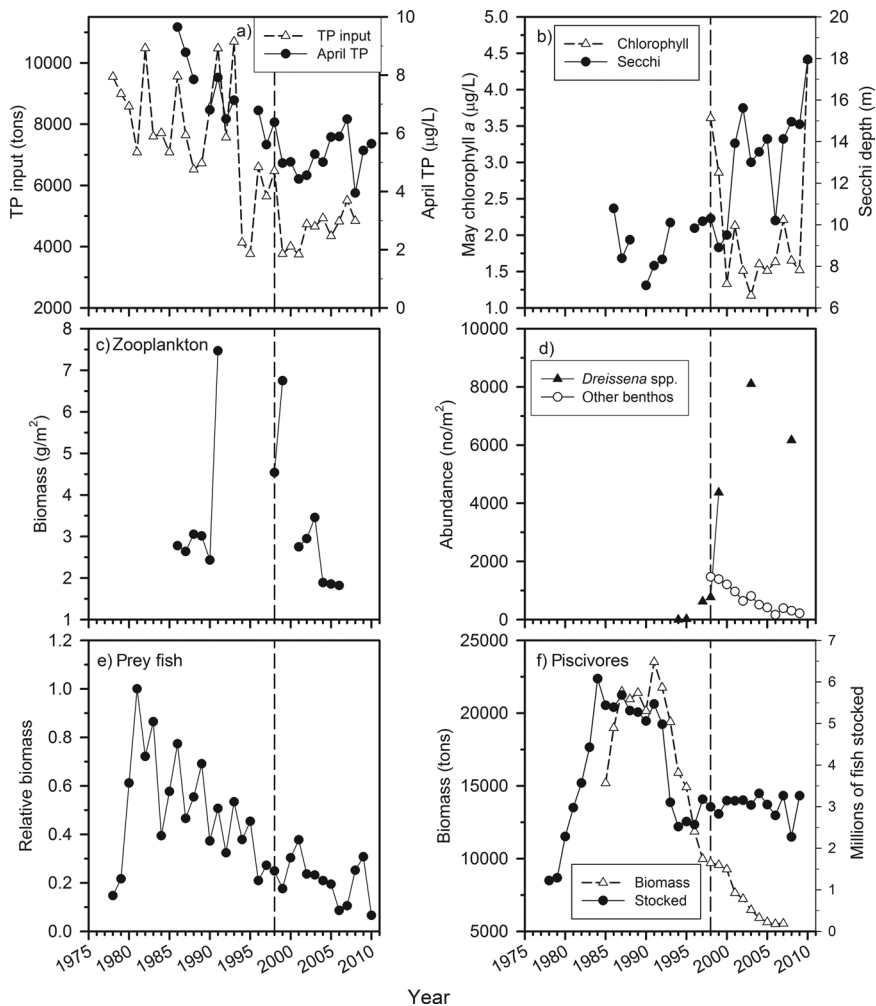


Figure 6. Time series of important physicochemical attributes and trophic levels in Lake Ontario. The lengths of the time series vary among the panels. The vertical dashed line at 1998 shows the point after which within-lake Spearman's rank correlations were analyzed. Abbreviations: g/m², grams per square meter; m, meters; no/m², number per square meter; TP, total phosphorus; µg/L, micrograms per liter. For details regarding data sources, see the supplemental material.

the presence of data limitations and gaps—as well as limitations to our analytical approach—that somewhat weaken our ability to draw robust conclusions.

First, in most of the lakes, our estimates of nutrients, benthic invertebrates, and zooplankton were collected farther offshore than where prey fish biomass was estimated. This highlights an unfortunate gap in nearshore monitoring and research that limits our understanding of how the watershed, nearshore, and offshore habitats are linked and influence one another (Seelbach et al. 2013). Second, although the use of satellite-derived estimates of chlorophyll *a* provides a comprehensive glimpse into phytoplankton dynamics within the epilimnion that cannot be achieved through *in situ* sampling, this method fails to characterize the dynamics in deeper water, such as the deep chlorophyll maximum. Third, the limited frequency (within each year) of the zooplankton sampling in all lakes but Erie could lead to underestimates

of the contribution of some species. Fourth, we chose to rely on prey fish data obtained only from bottom trawl sampling. Although acoustics and mid-water trawling are now used in most of the lakes to provide complementary estimates of prey fish biomass, data from these surveys were not available from all of the lakes after 1998. Fifth, the biomass estimates for key species in several trophic levels could not be included because of inadequate monitoring across the lakes (e.g., dreissenid mussels, planktivorous *Mysis relicta*, some piscivorous species). Sixth, pooling species at the community level can impede our ability to detect top-down or bottom-up effects that are occurring at the population level. Finally, we note that our correlations among trophic levels were generally limited to years including and after 1998 and that, when existing data sets permitted the analysis of older time series, we commonly obtained different results. As to whether these differences indicate changes in the nature of trophic interactions or whether they were artifacts resulting from small sample sizes in recent years is unclear. Given the complexity, size, and number of perturbations influencing the Great Lakes ecosystems, confidence in the present conclusions will be strengthened only by their corroboration with future data. Consequently, we would encourage revisiting these analyses as more data become available.

Although we should keep these caveats in mind, our analyses revealed a far greater prevalence of bottom-up regulation since 1998; 11 trophic interactions across the lakes and basins were consistent with bottom-up regulation, whereas only 1 interaction was consistent with top-down control. As a prerequisite for bottom-up regulation, TP inputs trended downward in all of the lakes but Superior between 1978 and 2008. April TP concentrations were more variable across these four lakes: there was no trend in central and eastern Lake Erie, but there was a positive trend in western Lake Erie between 1983 and 2010; there was a declining trend in Lake Ontario between 1986 and 1998 and between 1986 and 2010 (but not between 1998 and 2010); and there were declining trends for Lakes Michigan and Huron for both the entire time series and after 1998. These different responses can be explained, in part, by shorter retention times in Lakes Erie (about 3 years) and Ontario (about 7 years) relative to Lakes Huron (about

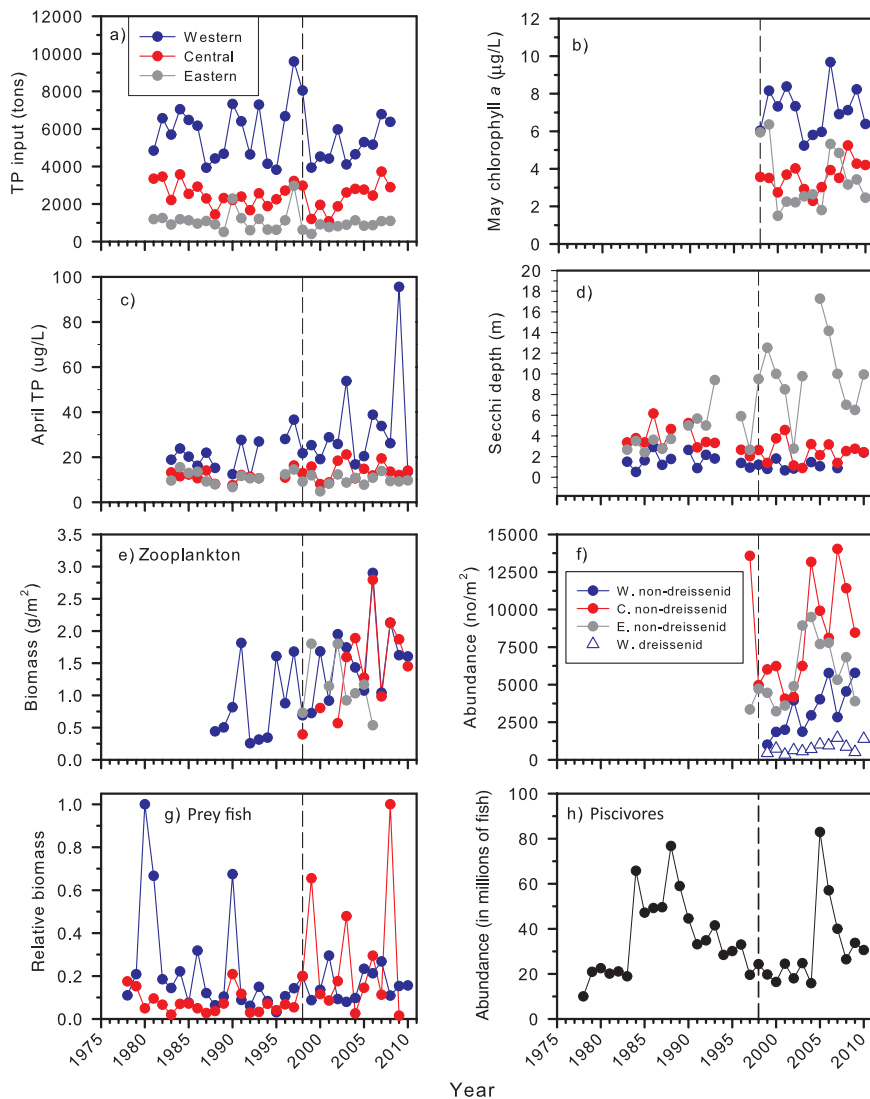


Figure 7. Time series of important physicochemical attributes and trophic levels in each basin (the western in blue, the central in red, and the eastern in gray) of Lake Erie, with the exception of piscivore abundance (panel [h]), which was estimated at the lakewide scale. The lengths of the time series vary among the panels. The vertical dashed line at 1998 shows the point after which within-lake Spearman's rank correlations were analyzed. Abbreviations: g/m², grams per square meter; m, meters; no/m², number per square meter; TP, total phosphorus; µg/L, micrograms per liter. For details regarding data sources, see the supplemental material.

16 years) and Michigan (about 59 years; Dobiesz et al. 2010). In addition, dreissenid mussels, which flourished earlier in Lakes Erie and Ontario than in Lakes Michigan and Huron, may help explain the more recent declines in the latter lakes through their influence on internal nutrient cycling (Hecky et al. 2004, Vanderploeg et al. 2010, Chapra and Dolan 2012).

A central question requiring further research involves determining the extent to which the trends observed in Lakes Huron, Michigan, and Ontario are driven by the proliferation of dreissenid mussels, which are now dominated by the quagga mussel in all of the lakes. Although these nonindigenous filter

feeders directly affect phytoplankton, we were unable to evaluate whether phytoplankton were under top-down control, given the lack of long-term, lakewide data in three of the four lakes in which they occur. Although the US Environmental Protection Agency began counting dreissenid mussels in 2007, their benthic monitoring program was designed for station-specific rather than whole-lake estimates. The limited spatial coverage of the program, in light of the potential spatial heterogeneity of dreissenid distributions, compromises the reliability of their lakewide population estimates. More extensive monitoring of the benthos has been undertaken by other agencies in Lakes Michigan, Huron, and Ontario, albeit at multi-year intervals. Therefore, among the data gaps that we mentioned, extensive annual sampling for dreissenids in each lake may well be the greatest one.

Dreissenid mussels can exert both direct, top-down control on phytoplankton by removing them through filtration and indirect, bottom-up control by sequestering phosphorus in shallower waters that otherwise may have been delivered to offshore phytoplankton. The former requires sufficiently large mussel densities and hydrodynamic conditions to maximize the delivery of phytoplankton to the bottom of the lake (e.g., during periods in which the water column is not stratified; Boegman et al. 2008, Fahnenstiel et al. 2010, Vanderploeg et al. 2010). The bottom-up control mechanism, however, has been hypothesized to occur when mussels in the nearshore (Hecky et al. 2004) or middepth regions (Vanderploeg et al. 2010) drive declines in nutrients and phytoplankton farther offshore, even during seasons in which

the water column is stratified (Cha et al. 2011, Pothoven and Fahnenstiel 2013). Our demonstration of lakewide chlorophyll *a* declines in Lakes Michigan and Huron between 1998 and 2010 for both the March–November and the July–September sampling periods (not presented here) suggest that both top-down and bottom-up regulation might be operating.

The strongest evidence for bottom-up control was observed in Lake Huron, because resource limitation was apparent for chlorophyll *a* (from April TP), zooplankton (from chlorophyll *a*), prey fish (from zooplankton), and piscivores (from prey fish). Despite the posited mechanisms of dreissenid impacts

Box 1. Common trends and key research questions in the Laurentian Great Lakes.

Several common trends emerged across three or more Great Lakes. Explanations for these trends and research questions that could improve our understanding of key drivers of food webs in the Great Lakes are provided below.

Since 1998, Lakes Superior, Michigan, and Huron have shown evidence of oligotrophication (e.g., clearer water, lower phytoplankton biomass). The proliferation of quagga mussels is a primary factor, because of their capacity to filter phytoplankton (Fahnenstiel et al. 2010, Vanderploeg et al. 2010). To a lesser extent, the binational Great Lakes Water Quality Agreement also led to long-term declines in phosphorus inputs in all lakes but Superior. In the future, researchers might explore why these trends were observed in Lake Superior, where dreissenid distributions were confined and where TP inputs have been without trend since 1978, or why they were not apparent in Lakes Erie or Ontario, where dreissenids do occur.

Nondreissenid benthic invertebrates declined in Lakes Michigan, Huron, and Ontario. Dreissenid mussels are viewed as the leading cause of the decline in native amphipods (*Diporeia* spp.); however, the exact mechanism remains uncertain (Nalepa et al. 2009). Interestingly, some shallow-water benthic invertebrates appear to benefit from dreissenid mussels, particularly on hard substrates (Stewart et al. 1998), which may explain the increased benthic invertebrate densities in western and central Erie.

Nonindigenous water fleas (e.g., *Bythotrephes*, *Cercopagis*) influence zooplankton communities. The establishment of predatory water fleas during the 1980s appears to have driven declines in herbivorous cladocerans in two ways: through direct predation and by inducing their migration into cooler, less productive waters (Pangle et al. 2007). In the future, researchers could explore how the effects of water fleas on zooplankton vary with productivity or how their effects compare with those of native predatory invertebrates (e.g., *Mysis relicta*, *Diacyclops thomasi*, *Limnocalanus macrurus*) that are commonly overlooked.

Time series have shown declines in prey fish in all of the Great Lakes but Erie and Ontario. Models that estimated the consumptive demand of top predators suggest that excessive piscivory could play a primary role (e.g., Jones et al. 1993, Negus 1995, Murry et al. 2010). Our analyses yielded evidence of top-down control in Lake Michigan but bottom-up limitation in Lakes Huron, Michigan, and Superior. Therefore, prey fish could be “squeezed” by adjacent trophic levels. In the future, researchers could explore whether bottom trawl catchability has changed with water clarity, repeat our analyses with acoustically derived estimates of prey fish, and evaluate other fish responses that would be consistent with top-down (e.g., truncated age distributions) or bottom-up (e.g., reduced growth, condition) regulation.

Can the estimates of top predators be improved? Piscivorous fish are difficult to sample with active gears that can estimate the number in a given area in a fishery-independent survey. Furthermore, estimates of natural reproduction require considerable effort to mark stocked fish. Given the importance of piscivores to fisheries and their potential to exhaust prey fish resources, researchers should prioritize deriving the best possible data to inform models that estimate their abundance and consumptive demand.

in the Great Lakes, the timing of events in Lake Huron raises questions as to whether the proliferation of mussels was the primary mechanism underlying the food-web changes that occurred in the 2000s. For example, the abrupt declines in offshore spring chlorophyll *a* (Barbiero et al. 2011), offshore cladoceran and cyclopoid zooplankton biomass (Barbiero et al. 2009), and prey fish (primarily alewife; Riley et al. 2008) occurred around 2003, before dreissenid mussels became abundant in depths greater than 50 meters. Furthermore, the available lakewide data reveal that the maximum densities of mussels in Lake Huron (1255 per square meter [m²] in 2007) were only a fraction of the maximum densities attained in Lakes Michigan (13,741 per m² in 2010) and Ontario (8106 per m² in 2003). However, the Lake Huron densities exclude Saginaw Bay, where dreissenids are probably reducing TP export into the main basin (Cha et al. 2011). Although the patterns elucidated in our analyses provide evidence for bottom-up control in Lake Huron (and, to some degree, in Lake Michigan) and although a recent ecosystem model in Lake Ontario also pointed to important bottom-up regulation (Stewart TJ and Sprules 2011), future research is required to improve our understanding of the mechanisms underlying the declines of key zooplankton and prey fish taxa and, especially, the role of nonindigenous mussels.

The only evidence for top-down control occurred between piscivore and prey fish in Lake Michigan. Modeling studies have similarly demonstrated top-down control of alewives in this lake (Stewart TW et al. 1981, Madenjian et al. 2005). The results from other modeling studies have indicated top-down control of rainbow smelt by piscivores in Lake Superior (Negus 1995, Bence et al. 2008) and top-down control of alewives by piscivores in Lake Ontario (Jones et al. 1993, Rand and Stewart 1998, Murry et al. 2010). These studies, coupled with reductions in piscivore growth rates in several of the lakes (Bence et al. 2008, He et al. 2008), prompted management agencies to reduce piscivore stocking in Lakes Ontario, Michigan, and Huron over different time periods during the past three decades (Eshenroder and Lantry 2013). With our correlation analyses, however, we were unable to detect top-down control of the prey fish communities in Lakes Superior, Huron, and Ontario.

Given the consistent top-down results of previous modeling studies, top-down control on the prey fish community could yet be occurring in lakes other than Michigan, in spite of our results. For example, in Lake Huron, piscivore biomass was relatively stable, whereas prey fish declined. One scenario under which top-down control could be operating despite no trend in piscivore biomass is that in which the energetic

content of prey fish declines and piscivores compensate by increasing prey fish consumption. In fact, the energy content of alewife has declined in Lake Michigan since the proliferation of dreissenid mussels and the decline of *Diporeia* (Madenjian et al. 2006). A second possible explanation for failure to document broader top-down control of prey fish is an elaboration on a previously mentioned data gap (i.e., piscivore biomass did not include some piscivore species or morphotypes in some lakes, including siscowet lake trout in Lake Superior and walleye, brown trout, Atlantic salmon [*Salmo salar*], coho salmon, and rainbow trout in Lakes Huron and Ontario). The addition of this biomass might have altered the apparent trends in piscivore biomass such that our correlation analyses could have yielded different results.

A comparison with other large aquatic ecosystems

Similar vulnerability to anthropogenic stressors and resultant changes in food-web structure have also triggered discussion regarding the importance of top-down and bottom-up regulation in the Great Lakes of eastern Africa (e.g., Kolding et al. 2008, Hecky et al. 2010, Witte et al. 2012). Lake Victoria offers one commonality with the Laurentian Great Lakes in that managers have successfully increased piscivore biomass. In contrast to the Laurentian Great Lakes, however, nutrient inputs and phytoplankton biomass have also been increasing during recent decades in Lake Victoria, as a result of population growth and development in the watershed.

Scientists in marine ecosystems have similarly debated the impact of bottom-up regulation and top-down control. In contrast to predictions from a recent analysis of marine ecosystems (Frank et al. 2007), we found minimal support for the hypothesis that warmer, high-species-richness systems (e.g., Lake Erie) are regulated by bottom-up forces, whereas colder, low-species-richness systems (e.g., Lake Superior) are regulated by top-down ones. These results should certainly be revisited, especially as improved data sets become available. Interestingly, using a more mechanistic approach than ours, Bence and colleagues (2008) used piscivore growth rates and ratios of predator biomass to prey fish biomass to show that, among four of the Great Lakes, the evidence for top-down control was strongest for Lake Superior and weakest for Lake Ontario, which is consistent with Frank and colleagues' (2007) conclusions.

One other similarity to explore between the Great Lakes and marine ecosystems is the importance of intermediate trophic levels. In coastal marine ecosystems, small planktivorous pelagic fishes can have large ecosystem impacts owing to their capacity to limit the production of piscivores (through conventional bottom-up control and their capacity to prey on the larval life stage of piscivores) while exhibiting top-down control on zooplankton (Bakun 2006, Fauchald et al. 2011). Because the species richness of these planktivorous fishes is also "slim" relative to the more diverse adjacent trophic levels, the term *wasp-waist control* has been coined to describe these ecosystems and interactions (Cury et al. 2000). Perhaps the best example of a species that fits

the wasp-waist analogy in the Laurentian Great Lakes is nonindigenous alewife (native to the Atlantic Ocean), which can structure zooplankton prey through planktivory (e.g., Wells 1970), depress piscivore populations (e.g., lake trout) through predation on their larval stage (Krueger et al. 1995) or facilitation of thiamine deficiency (see Riley et al. 2011), and contribute disproportionately to internal phosphorus cycling (e.g., Kraft 1993). The collapse of alewife in Lake Huron during the early 2000s led to a resurgence in native predators, such as walleye (Fielder et al. 2010) and lake trout (Riley et al. 2007). Several conceptual models (like the wasp-waist one) have been proposed in the Laurentian Great Lakes to improve the understanding of ecosystem dynamics (e.g., Hecky et al. 2004, Vanderploeg et al. 2010). We encourage not only the evaluation of these models (*sensu* Cha et al. 2011) but also a discussion regarding whether models developed in marine ecosystems are applicable to the Great Lakes.

Conclusions

Our analyses suggest that bottom-up regulation has been more prevalent than top-down regulation in the Laurentian Great Lakes during recent decades. Such control probably emanated from long-term declines in TP inputs and the more recent proliferation of nonindigenous mussels, which can sequester nutrients in shallower waters. The lake with the strongest evidence for bottom-up regulation was Lake Huron, followed by Lake Michigan. Evidence for bottom-up regulation was observed in only one trophic interaction for Lake Superior, western Lake Erie, and Lake Ontario. We encourage future mechanistic research to test these correlative findings, continued monitoring to extend the time series used here, and efforts to alleviate some of the identified data gaps. Such efforts would accelerate the ability of managers to implement ecosystem-based management approaches and would offer scientists and managers the best arsenal to meet coming challenges (e.g., climate-driven changes to aquatic habitat, additional nonindigenous species) that could lead to the degradation of these valuable inland seas.

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Supplemental material

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